American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2208 FEBRUARY 17, 1965

The Neotropical Genus *Labiotermes* (Holmgren): its Phylogeny, Distribution, and Ecology (Isoptera, Termitidae, Nasutitermitinae)

By Alfred E. Emerson[1] and Frank A. Banks[2]

INTRODUCTION

Labiotermes is a distinctive genus of South American termites at present containing the type species, *L. labralis* (Holmgren), and three more species, *L. longilabius* (Silvestri), *L. brevilabius*, new species, and *L. pelliceus*, new species.

Emerson (1955, p. 514) assigned two named species and three new species to *Labiotermes*, but subsequent study indicates that one of the designated new species is a variant of the type species of the genus, *L. labralis*, and does not warrant taxonomic rank. The other two new species are described in the following pages.

Emerson (1955, p. 468) categorized *Labiotermes* as a relatively primitive endemic genus, belonging to a successful specialized subfamily (Nasutitermitinae), which was unable to disperse from the region of origin (Neotropical) when climatic and topographical highways were available, probably because of competitive biotic barriers.

[1] Research Associate, Department of Entomology, the American Museum of Natural History, New York; Professor Emeritus, Department of Zoology, the University of Chicago.

[2] Associate Professor of Biology, Chicago City Junior College, Crane Branch, Chicago, Illinois.

ACKNOWLEDGMENTS

The present paper is a portion of studies that are supported by grants from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago, the John Simon Guggenheim Foundation, the New York Zoological Society, and the National Science Foundation (Grants NSF-G3266 and NSF-G25146).

Mrs. Eleanor Fish Emerson gave valued assistance in the preparation of the manuscript.

We are also indebted to the following individuals for specimens: the late Mr. A. M. Adamson, Mr. P. J. Anduze, Mr. R. L. Araujo, Mr. E. R. Blake, the late Mr. G. E. Bodkin, the late Dr. Nils Holmgren, the late Dr. W. M. Mann, Mr. A. Ries, the late Dr. A. Roman, Dr. C. H. Seevers, the late Dr. F. Silvestri, Dr. T. E. Snyder, Dr. N. Weber, and Mr. S. Weinstein.

Unless otherwise stated, all specimens were determined by Alfred E. Emerson and are deposited in the American Museum of Natural History. Duplicate specimens have been deposited in numerous major collections throughout the world.

GENUS *LABIOTERMES* HOLMGREN

< Genus *Cornitermes* SILVESTRI, 1901, p. 4.
< Genus *Cornitermes* SILVESTRI, 1903, p. 52.
< Genus *Termes* DESNEUX, 1904, pp. 26, 28.
< Subgenus *Termes* DESNEUX, 1904, pp. 32, 35.
< Genus *Cornitermes* HOLMGREN, 1906, p. 549.
< Genus *Cornitermes* HOLMGREN, 1912, pp. 45, 49.
< Subgenus *Labiotermes* HOLMGREN, 1912, p. 50.
< Genus *Cornitermes* EMERSON, 1925, p. 363.
< Subgenus *Labiotermes* EMERSON, 1925, p. 363.
< Genus *Cornitermes* SNYDER, 1926, p. 17.
= Subgenus *Labiotermes* SNYDER, 1926, p. 17.
< Genus *Labiotermes* SJÖSTEDT, 1926, p. 150.
< Subgenus *Labiotermes* EMERSON, 1928, p. 406.
= Genus *Labiotermes* SNYDER, 1949, p. 334.
= Genus *Labiotermes* EMERSON, 1952b, pp. 481, 482, 484, 485, 490, 503, 508.
= Genus *Labiotermes* EMERSON, 1955, pp. 495, 514.
= Genus *Labiotermes* SANDS, 1957, pp. 14, 22.

TYPE SPECIES: *Cornitermes labralis* Holmgren (1906, p. 549; Sjöstedt, 1926, p. 150).

STRUCTURE AND PHYLOGENY: *Labiotermes* is related to *Paracornitermes* Emerson (*in* Snyder, 1949, pp. 333, 377; Araujo, 1954, pp. 181-189) and to *Armitermes* Wasmann near the base of the branch of the Nasutitermitinae that diverged from the main branch from a stock related to *Syntermes*

and *Procornitermes* (Ahmad, 1950; Emerson, 1952b; 1955, p. 495; 1961, p. 120, fig. 4). *Labiotermes* resembles *Paracornitermes* and *Armitermes* in the imago-worker mandibles, all of which possess a relatively large apical tooth compared with those genera (*Syntermes*, *Procornitermes*, *Cornitermes*, *Rhynchotermes*, *Nasutitermes*, *Trinervitermes*, and others) on the other branch of the Nasutitermitinae (Emerson *in* Allee *et al.*, 1949, p. 727, fig. 263; Ahmad, 1950). Also the cutting edge of the left mandible, between the first (plus fused second) marginal tooth and the third marginal tooth, is undulating in *Labiotermes* and its relatives in distinction to the generally evenly concave cutting edge of the left mandible of the genera of the *Syntermes-Nasutitermes* branch. These characters are distinctive in the genera with mandibulate soldiers in both branches of the phylogenetic tree. The derived genera with nasute soldiers in some cases are less distinctive in these imago-worker mandibular characters, probably as the result of convergence or parallel evolution.

The enlarged labrum of the soldier of *Labiotermes* was doubtless the character from which the generic name was constructed. *Paracornitermes* and *Labiotermes* together have a similarly large labrum compared with that of the soldiers of their relatives on both branches of the Nasutitermitinae. The mandibular teeth of the soldier of *Labiotermes* resemble those of *Procornitermes* and *Cornitermes* (Emerson, 1952b), but the reduction of the teeth may be parallel rather than homologous.

The teeth on both soldier mandibles of *Paracornitermes* (Emerson, 1952b; Araujo, 1954) are fairly large and prominent and are double-pointed. The two points of the marginal tooth on the right mandible are close together but are relatively wide apart on the left mandible. What appear to be homologous double-pointed teeth occur in both mandibles of the soldiers of the more primitive species of *Armitermes*. *Labiotermes* shows a basic homology of the teeth of the soldier mandibles in *Paracornitermes*, *Armitermes*, and *Curvitermes*, even though the dentition is reduced in *Labiotermes*.

The frontal tube or projection at the gland opening on the head of the soldier of *Labiotermes* is larger than that of *Syntermes* and smaller than that of *Procornitermes* and *Cornitermes*. The frontal projection on the head of the soldier of *Paracornitermes* is similar in proportional size to that of *Labiotermes*, while *Armitermes* has a much larger frontal projection and is a transitional genus on this branch between the more primitive mandibulate soldiers of the subfamily and the more advanced nasute soldiers with vestigial mandibles. Nearly all species of *Armitermes* have larger marginal teeth in the soldier mandibles, although *A. heterotypus* Silvestri and *A. parvidens* Emerson and Banks (1957, pp. 6–11) have small marginal teeth.

The V-shaped notch in each soldier mandible of *Labiotermes*, without teeth that project markedly beyond the continuation of the cutting edge, is a good distinguishing character of the genus and is combined in a consistent association with other characters of the frontal projection or tube, mandibles, labrum, and postmentum. The postmentum is constricted toward the rear, and the sides of the anterior two-thirds are prolonged laterally into sharp ridges that cover the lateral sutures when the head is viewed from below.

Paracornitermes seems to be the closest genus to *Labiotermes* and may be considered to be somewhat more primitive in most general characters. *Paracornitermes* is also the most primitive genus on the *Paracornitermes-Subulitermes* branch of the Nasutitermitinae and seems to be most closely related to *Procornitermes* on the *Syntermes-Nasutitermes* branch. *Labiotermes*, however, is more primitive than any other genus in the subfamily except *Syntermes* in having 16 to 17 articles in the antenna of the imago and 15 to 16 articles in the antenna of the soldier. The evolutionary direction of numbers of antennal articles is always toward reduction in termites (Emerson, 1962), so that it seems probable that *Labiotermes* evolved from stock somewhat more primitive than *Procornitermes* and *Paracornitermes*, and somewhat more advanced than *Syntermes*, the most primitive known genus of the subfamily (Emerson, 1952b, pp. 484–485). The tibial spurs of *Syntermes* and some species of *Procornitermes* are 3:2:2, while most species of *Procornitermes* and all species of *Cornitermes*, *Paracornitermes*, and *Labiotermes*, and the more advanced genera on both branches of the Nasutitermitinae have two tibial spurs on each leg (2:2:2). The presence of three spurs on the front tibia is considered to be a primitive character, and two spurs a derived character, in the family Termitidae (Emerson, 1962).

Labiotermes, therefore, is primitive in some respects and derivative in other respects. The theoretical origin of *Labiotermes* from an extinct group that arose later than the ancestor of *Syntermes* agrees with the known facts. After the establishment of the imago-worker mandible of the *Paracornitermes* and *Labiotermes* type, these genera seem to have diverged, each retaining some primitive characters and showing advancement in others, so that neither can be considered to be directly ancestral to the other.

Because of the reduction of the mandibular teeth in the soldier of all species of *Labiotermes*, this genus cannot be directly ancestral to *Armitermes*, but *Paracornitermes* is either a direct ancestral genus to *Armitermes* or is little modified from the extinct ancestral genus. Such a statement does not imply that evolution at the species level has not taken place, but only that the common ancestor, if known, would probably be placed in the genus *Paracornitermes*.

Because of neozoological considerations discussed in the following pages, it may be surmised that the evolution of the ancestral types of the Nasutitermitinae closely allied to the modern genera with mandibulate soldiers had already taken place during the Cretaceous period, probably at least by mid-Cretaceous times. Otherwise it is difficult to explain the presence of derived genera with nasute soldiers on both branches of the phylogenetic tree of the Nasutitermitinae in all the tropical zoogeographical regions of the world.

On the basis of comparisons with more primitive genera, it might be possible to indicate primitive and derived species within the genus (Emerson, 1962, p. 21). Among termites, the phylogenetic relations of the species within any genus are seldom understood, the data are usually meager and open to alternative explanations, and few authors hazard any interpretations. The species of *Labiotermes* show only a few known characters on which tentative hypotheses can be built, and the pattern of associated characters is not wholly consistent. The characters that might indicate a relative phylogenetic order are (1) the number of articles in the antenna which always shows phylogenetic reduction in termites; (2) the relative size of the head which is usually larger in the more primitive species; (3) the relative length of the projection of the frontal gland which is usually smallest in the more primitive species and largest in the adaptively advanced species; (4) the pilosity of the head, particularly of the soldier, which possibly represents a phylogenetic order from moderately abundant scattered bristles toward either a reduction on the one hand or an increase on the other hand; (5) the small hump or prominent projection at the base of the front coxa which is not found in the more primitive genera and therefore probably represents a phylogenetic advance; (6) the more forward position of the opening of the frontal gland on the head of the soldier which is probably an advanced character; and (7) the raised portion of the head of the imago in the vicinity of the fontanelle which is possibly a derived character. No other species characters as yet discovered within the genus seem to provide a clue to their phylogeny.

One may guess that *Labiotermes labralis* is nearer to the base of the phylogenetic tree of the genus than the other known species because it is larger; the antenna of the imago in some cases has 17 articles and that of the soldier in some instances has 16 articles; the projection at the opening of the frontal gland of the soldier is shorter, smaller, and set farther back on the head than in other species; and the projection at the base of the front coxa is absent or at most represented by a flat, slightly convex hump. The sparse bristles on the soldier head, however, may

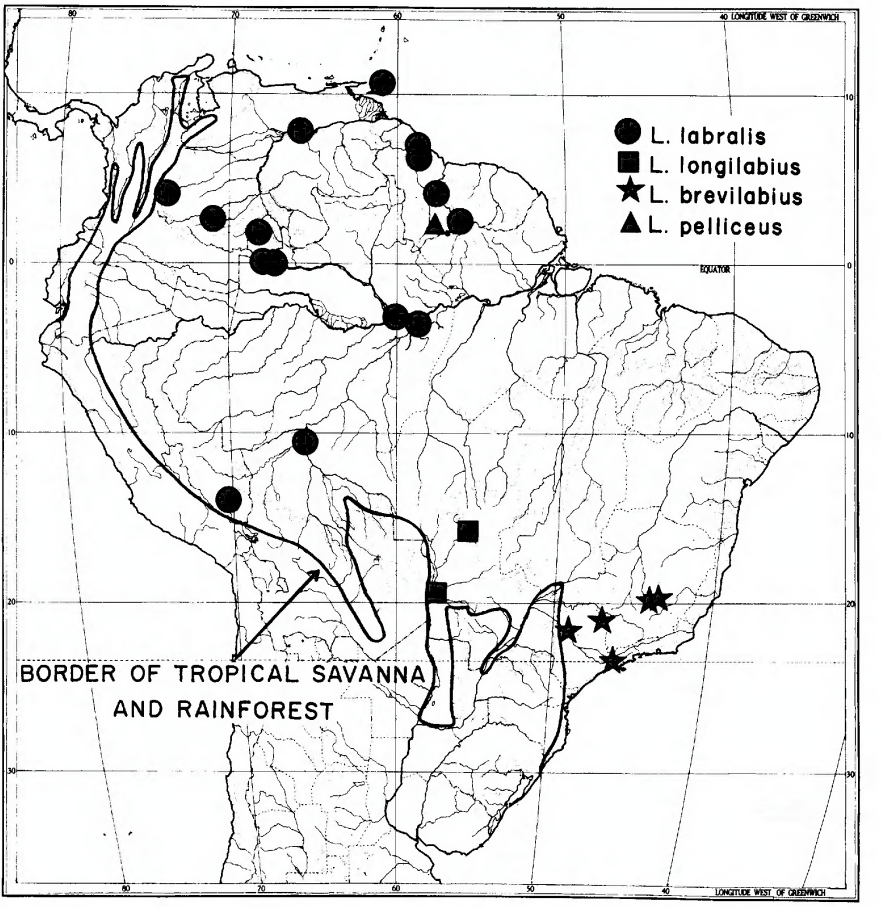

FIG. 1. Distribution of the species of the genus *Labiotermes*, showing the approximate border of the tropical savanna and rain forest combined.

indicate some reduction from the pilosity of the more primitive ancestor.

The habitat of *L. labralis* is the Neotropical rain forest. The range of the species (fig. 1) is probably coextensive with the relatively high soil humidity and temperature of this biome. The tropical rain forest is the optimum environment for the greatest abundance and variety of termite species (Emerson, 1955, p. 473), and may be presumed to be the habitat from which major adaptive radiation to savannas, steppes, and temperate regions occurred. In the case of *Labiotermes*, the genus may have originated in the tropical rain forest and later have given rise to the southern savanna and dry-forest species (fig. 1). The data, however, are insufficient for any

final conclusions concerning these ecological adjustments to be drawn.

Labiotermes longilabius, *L. brevilabius*, and *L. pelliceus* indicate closer relationships among themselves than any of these species shows to *L. labralis*.

Because of the larger size and the less sharp coxal projections, *L. longilabius* may be the most primitive of these three species, with *L. brevilabius* somewhat more derivative but closely related to *L. longilabius*. *Labiotermes pelliceus* from the moderately elevated rain forest of British Guiana, because of its abundant covering of bristles and hairs on the soldier head, may be considered to be the most advanced of these three species, with *L. longilabius* its closest relative.

The suggested relationships of the species are highly speculative and should serve only as hypotheses to be tested by the accumulation of more relevant data.

NESTS AND BEHAVIOR: A nest of *L. labralis* was found by A. E. Emerson at Kartabo, British Guiana, at the base of a tree in a moist and rather swampy portion of the rain forest. Another nest with a queen was found on an old stump in a somewhat drier portion of the same forest. A nest was found by A. E. Emerson several miles from St. Joseph, Trinidad, on a bank of a road rather high up in the hills near a cacao plantation in an area presumed to have been originally covered by rain forest. Some variation in soil moisture seems to be tolerated or brought under control by this species.

The nests were made of dirt carton that had probably passed through the intestines of the workers. The Trinidad nest was about 1½ feet wide, 2 feet long, and 2 feet high. The cells were large in all the nests, and the inside surface (plaster) of all the cells and passageways was deeply pitted or sculptured—a characteristic not observed for any other New World termite so far known. Pitting of the internal lining of the nest cells has also been observed in the nests of *L. labralis* at Kartabo, British Guiana, and by S. Weinstein in nests of the same species in Colombia. Species from Africa of a series of genera related to *Apicotermes* (Grassé and Noirot, 1954), *Postsubulitermes parviconstrictus* Emerson in the Congo (Emerson, 1960b, p. 14), and an undetermined species on the *Subulitermes*-branch with a small nasute soldier in Sarawak have somewhat similar sculpturing of the cell and gallery walls. The function of this type of construction is unknown.

In all cases observed by A. E. Emerson, the entire nest was above ground level, and the queen occupied a hard portion of the nest near the center. The royal cell was not much larger than the other cells of the nest. The abdomen of the workers was enlarged and filled with mud and sand. It seems likely that the source of nourishment is the organic matter

or humus in the soil that the termites eat rather than dead wood. The nest is probably constructed of this excrementous dirt. The workers and soldiers are quite slow in their movements compared with those of *Cornitermes pugnax* Emerson and most other species of Termitidae, with the notable exceptions of a few species such as *Angularitermes nasutissimus* Emerson from British Guiana and *Tarditermes contracolor* Emerson from the Congo.

Alates of *L. labralis* were found flying at 7 P.M. on May 12, 1924, at Kartabo, British Guiana.

Silvestri (1903) described the nests of *L. longilabius*. This species builds underground nests with large cells lined with blackish carton and no definitive royal cell. It is believed that it eats earth and vegetable detritus.

R. L. Araujo (notes on label) described the nest of *L. brevilabius* from Novo Horizonte, São Paulo, Brazil (No. 2652), as "sandy nest of uniform structure."

ECOLOGY AND DISTRIBUTION: The genus as a whole seems to be adjusted to moderately dry and to wet soils. *Labiotermes longilabius* overlaps the range of *Paracornitermes laticephalus* at Coxipó near Cuiabá, Brazil. According to Silvestri (1903), *L. longilabius* lives in dry places with arboreal vegetation. Araujo (1954, p. 182) described the vicinity of Cuiabá (latitude 15° 36′ S., longitude 56° 11′ W.), Mato Grosso, Brazil. The elevation is 219.5 meters, the average annual temperature is 26° C., and the average annual precipitation is 1425 mm. Cuiabá lies within the general savanna formation called "*campos cerrados*" and is characterized by Warming (1925, p. 296) as low, open, sunny forest, composed of bent and tortuous deciduous trees, together with a rich vegetation of grasses, perennial herbs, and small scattered shrubs that cover the ground.

Labiotermes brevilabius from the states of São Paulo and Minas Gerais, Brazil, is found in a region with between 1013 and 1315 mm. of precipitation. The average annual temperature of the city of São Paulo is 18° C. (Araujo, 1958a, 1958b). The vegetation is dry tropical forest of semideciduous and deciduous, broad-leaved trees throughout the known range of the species.

The other two species of the genus, *L. labralis* and *L. pelliceus*, are from lowland and upland rain forest. Some records of *L. labralis* are from rain forests that border tropical savannas or from gallery forests (Bates, 1948). The average annual precipitation at sea level at Kartabo, British Guiana, is about 2575 to 2660 mm., and the average annual shade temperature is 26.5° C. The vegetation is dense lowland rain forest, with no natural savannas in the area (Beebe, 1925; Davis and Richards, 1933–1934; Fanshawe, 1952). The vegetation at Itabu Creek, upper New River, in the Acary Mountains of British Guiana near the Brazilian border is

tropical rain forest at an elevation of about 610 meters. The termite fauna of Itabu Creek and the New River area has a number of distinct species not found during a thorough search at Kartabo (Emerson, 1925) at the junction of the Mazaruni and Cuyuni rivers in British Guiana, and presumably there is a small difference of the habitat within the continuous rain forest. The vegetation of Villavicencio, Colombia, is both savanna and forest at the foot of the Andes. The town is 500 meters above sea level, with an average annual rainfall of between 3964 mm. and 4987 mm. The annual mean temperature is 26.5° C. (Bates, 1948).

The northern distribution of *Labiotermes* resembles that of several genera found in tropical or subtropical South America that have not passed beyond the Andean barrier into Panama. These genera were briefly discussed by Emerson (1952b, p. 508; 1955, pp. 468, 495). Some, such as *Syntermes*, are modified slightly if at all from their Cretaceous ancestors which did not disperse to the Old World at the time when some of their derived genera (*Nasutitermes* and relatives of *Angularitermes* and *Subulitermes*) did. Instead, they remained in isolated Tertiary South America and doubtless speciated to some degree. When Pliocene land connections made it ecologically and topographically possible to invade Central America, some genera, such as *Cornitermes* and *Armitermes*, managed to do so, while other genera, such as *Syntermes* and *Labiotermes*, did not. The Andes presented a major climatic and topographical barrier to dispersion through the Tertiary, but it seems probable that some species moved along the northern coast which acted as a "filter bridge" in the late Pliocene, Pleistocene, and recent times. Very few species of termites are found on both sides of the Andean barrier either in the south or in Colombia.

It remains a puzzle why the genera of Nasutitermitinae with mandibulate soldiers failed to disperse to Asia during tropical climatic connections over the Bering land bridge in the Cretaceous, when circumstantial evidence indicates that the genera with nasute soldiers spread to the Old World through the tropical Orient to Australia, Africa, and Madagascar. There seems to be no physical or climatic reason for this difference in dispersal, so that it is suggested that the evolution of improved defense in the convergent nasute soldier may have enabled the advanced genera to push through competitive barriers that produced biotic boundaries for the genera with mandibulate soldiers (Emerson *in* Allee, *et. al.*, 1949, p. 726; Emerson, 1961, p. 121).

TERMITOPHILES: Seevers (1957) has published a monograph of the termitophilous Staphylinidae, including an account of the reciprocal phylogeny of these beetles with their host termites. Five species of beetles,

belonging to two tribes, have been found associated with *Labiotermes*. All the species are non-physogastric except one, *Termitosymbia nitida*. All five species have been found only with *L. labralis* but are recorded from separate portions of the range of this variable species. The phylogenetic relations of two genera and four species of beetles in the nests of *Labiotermes* show perfect consistency with the phylogeny of their host genus. The subtribe Termitozyrina of the tribe Myrmedoniini contains seven known species placed in five genera. The host of *Termitophagus synterminus* Silvestri was determined by Silvestri as *Syntermes grandis*. More recently R. L. Araujo has collected the same beetle from host nests that he determined as those of *Syntermes wheeleri* in the state of São Paulo. Because of the locality, it is probable that Silvestri's determination of the host is an error. The host of *Termitonusa sequax* Borgmeier is *Procornitermes araujoi* from the state of Goiás, Brazil. This host was also originally misdetermined as *Cornitermes similis*. The host of *Iheringocantharus ypiranganus* Bernhauer is *Syntermes wheeleri* from the state of São Paulo. The host species of *Termitozyras adamsoni* Seevers is *Labiotermes labralis* from Trinidad. The host of *Termitozyras guianae* Seevers is *Labiotermes labralis* from British Guiana. The host of *Termitozyras boliviae* Seevers and *Termitosymbia nitida* Seevers is *Labiotermes labralis* from Bolivia.

The correlation of the taxonomic relations of these genera of termitophiles and the genera of their host termites is completely consistent. The phylogeny of the termitophiles seems to be closely parallel to the phylogeny of their hosts as interpreted in the preceding discussion. We have strong indications of the evolution over millions of years of an interspecies ecosystem, with adjustment of one species to another and both to a socially controlled physical and biotic habitat within the termite nests. The evolution of the termitophiles has been directed toward adaptation to their hosts and nest habitat, but there is no indication that the termites have evolved adaptations to the termitophiles.

The occurrence of geographically separated species of termitophiles associated with a single widely dispersed host species is not unique. Several instances were reported by Seevers (1957) in his lists of termitophiles, hosts, and localities. Also a number of cases are known in which more than one congeneric species of termitophile may be found with a single host species of termite from the same locality—sometimes even from the same nest. Unless all these species associations are the result of errors in taxonomy, it must be assumed that the isolating factors, the adaptive distinctions, and the rates of evolutionary change may be different in the termitophiles compared with those of their hosts. It would be remarkable if such differences in the operation of evolutionary factors on

separate species in ecological associations did not exist, even when the species have had a reciprocal phylogeny for millions of years.

The other known termitophilous beetle associated with *Labiotermes* is placed in the subtribe Termitonannina. It was found with *L. labralis* in Arena Forest, Trinidad, and was assigned by Seevers (1957) to the species *Termitocomes trinidadensis* Seevers. Another species of the same genus, *Termitocomes wasmanni* Seevers, was found in the nest of *Speculitermes silvestrii* (Emerson) at Kartabo, British Guiana. The rare soldier caste of one Oriental species of *Speculitermes* has recently been reported by Roonwal and Chhotani (1960b). The Neotropical species assigned to *Speculitermes* lack a soldier caste, and future study will probably show that they should be placed in at least two new genera allied to *Speculitermes* and *Anoplotermes*. *Anoplotermes* from the Neotropical and Ethiopian regions also lacks soldiers but shows relationships to the Oriental *Eurytermes* with a soldier caste. *Anoplotermes shillongensis* from India, described by Roonwal and Chhotani (1959, 1960a, 1962) from the worker caste alone, is, in our opinion, probably a species of one of the closely allied Oriental genera.

Eurytermes, *Speculitermes*, *Anoplotermes*, and their allies clearly belong to the Amitermitinae and are not closely related to the Nasutitermitinae, which include *Labiotermes*. Seevers (1957) places six genera of Neotropical termitophiles in the subtribe Termitonannina of the tribe Termitonannini. The hosts belong to the termite genera *Anoplotermes* and *Speculitermes* (Amitermitinae), and *Syntermes*, *Procornitermes*, *Cornitermes*, *Labiotermes*, and *Subulitermes* (Nasutitermitinae). The Amitermitinae are the most primitive subfamily of the Termitidae in most of their characters and probably originated in the tropical Orient. The Nasutitermitinae are the most advanced subfamily of the Termitidae and almost certainly originated in the Neotropical Region.

In contrast to the termitophiles of the subtribe Termitozyrina and their termite hosts, the termitophilous subtribe Termitonannina does not show a clear reciprocal phylogeny with its hosts (Seevers, 1957, p. 46). There are several possible explanations for this discrepancy. 1. The taxonomic relationships described might not be based on homologous structures, but this explanation is unlikely in view of the meticulous phylogenetic studies of the beetles and their hosts and the remarkable phylogenetic consistency of the large majority of termitophiles with their hosts. 2. There may be numerous inaccurate associations of termitophiles and hosts through errors of collecting or determination. Doubtless some errors of this sort confuse the records and obscure some of the actual correlations between termitophile and host phylogenies, but, if such is

the case for the subtribe Termitonannina, there seems to be an improbable bunching of errors. 3. The third possibility, and the one favored by the present authors, is that some groups of termitophiles have changed hosts through ecological and geographical proximity during their evolutionary history. Although a high proportion of termitophile evolution has followed the branching of the phylogenetic tree of their hosts, it seems probable that some of the groups are more "host labile" than others through the tens of millions of years of Cretaceous and Tertiary history.

Key to the Species of the Genus *Labiotermes*

Imago

1. With small triangular or elliptical light fontanelle spot (fig. 2); width of head, 1.88–2.09 mm.; diameter of eye, 0.63–0.77 mm. ..... *L. labralis*
   Fontanelle spot oval or slit-shaped 2
2. Fontanelle spot oval, light yellow, forked at tip (fig. 5); width of head, about 1.75 mm.; diameter of eye, about 0.59 mm. ..... *L. longilabius*
   Fontanelle relatively inconspicuous, narrow, slit-shaped (fig. 7); width of head, 1.56–1.59 mm.; diameter of eye, 0.47–0.49 mm. ..... *L. brevilabius*

Soldier

1. Conspicuous hump or small projection on the outer side of the front coxa near its base (fig. 9D) 2
   Base of front coxa with an inconspicuous flat hump ..... *L. labralis*
2. Head sparsely covered with bristles or hairs 3
   Head thickly covered with bristles and hairs (fig. 9A, B) ..... *L. pelliceus*
3. Labrum proportionately long (fig. 6) ..... *L. longilabius*
   Labrum proportionately short (fig. 8) ..... *L. brevilabius*

Labiotermes labralis (Holmgren)

Cornitermes labralis Holmgren, 1906, p. 553 (imago, soldier, worker), fig. N (imago), fig. O (soldier), fig. P (worker).

Cornitermes labralis Holmgren, 1909, p. 80 (anatomy), fig. 15 (imago).

Cornitermes (*Labiotermes*) *labralis* Holmgren, 1912, pp. 50, 51 (systematics), fig. 22 (soldier mandibles).

Cornitermes (*Labiotermes*) *labralis* Emerson, 1925, pp. 311 (soldier), 363 (imago, soldier), fig. 47 (imago, soldier).

Cornitermes (*Labiotermes*) *labralis* Snyder, 1926, p. 20 (locality).

Eutermes labralis Sjöstedt, 1926, p. 150 (systematics).

Labiotermes labralis Sjöstedt, 1926, p. 150 (systematics).

Cornitermes (*Labiotermes*) *labralis* Adamson, 1937, pp. 2, 5 (biology).

Labiotermes labralis Snyder, 1949, p. 334 (synonymy).

Labiotermes labralis boreus Emerson *in* Snyder, 1949, p. 334 (synonymy).

Labiotermes labralis Ahmad, 1950, p. 82 (locality), fig. 11 (imago-worker mandibles).

Labiotermes labralis labralis Emerson, 1952b, p. 490 (termitophiles).

Labiotermes labralis boreus EMERSON, 1952b, pp. 481, 490, 510 (biology, termitophiles).

Labiotermes labralis boreus SNYDER, 1956, pp. 191, 195 (locality), 197 (soldier), 200 (imago).

Labiotermes labralis SEEVERS, 1957, pp. 189, 232, 240, 241, 242, 294, 298, 303 (termitophiles).

IMAGO (FIG. 2): Head light to dark brown or reddish brown, usually lighter in front; postclypeus and basal articles of antennae same color as

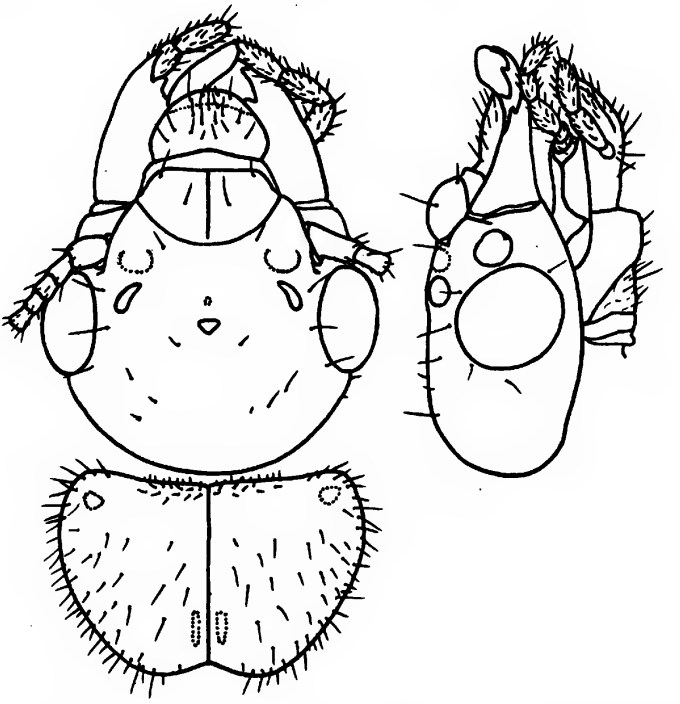

FIG. 2. Female imago of *Labiotermes labralis* (Holmgren), upper New River, British Guiana; head and pronotum from above and head from the side.

front of head; fontanelle spot light yellow or white; labrum yellow, with hyaline tip; pronotum light brown, in general lighter than head; under side of thorax, coxae, and femora yellow; tibiae light brown, noticeably darker than femora; wings light yellow-brown, costal border and radius dark brown at base and yellow near tips; anterior tergites light brown, about color of pronotum; last three tergites and middle hind portion of seventh tergite light brownish yellow or orange; sternites ranging from light brownish yellow in front to light brownish orange in the rear,

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF TWENTY-THREE IMAGOES OF *Labiotermes labralis* (HOLMGREN)

	Morph-otype, Peru	Para-morph-otype, Peru	Itabu Creek, British Guiana	Rockstone, Kartabo, British Guiana, Trinidad	Villavi-cencio, Colombia
Length of head to tip of labrum	2.06	2.09	2.06-2.18	—	—
Length of head to side base of mandible	1.65	1.65	1.47-1.56	—	—
Width of head	1.97	2.00	1.88-1.94	1.90-1.96	2.00-2.09
Length of fontanelle	0.12	0.14	0.10-0.15	—	—
Width of fontanelle	0.11	0.15	0.10-0.12	—	—
Fontanelle from ocellus	0.41	0.41	0.38-0.44	—	—
Diameter of eye	0.74	0.72	0.63-0.65	0.67-0.77	0.76
Eye from lower margin	0.04	0.05	0.09	—	—
Ocellus from eye	0.12	0.08	0.12-0.14	0.04-0.11	0.07-0.09
Length of ocellus	0.24	0.24	0.19-0.22	0.24-0.29	0.26
Width of ocellus	0.18	0.20	0.14-0.16	0.21-0.22	—
Length of postclypeus	0.47	0.44	—	—	—
Width of postclypeus	0.79	0.82	—	—	—
Length of pronotum	1.09	1.06	0.98-1.00	0.90-1.00	1.06
Width of pronotum	1.65	1.68	1.59-1.72	1.53	—
Length of hind tibia	2.82	3.18	2.56-2.76	2.88	—
Length of forewing scale	1.29	1.18	1.06-1.10	—	—
Length of forewing from suture	—	—	—	16.00-16.80	—
Width of forewing	—	—	—	4.90-5.35	—

lighter than tergites, margins lighter than middle. Sparsely scattered, medium long hairs on head, postclypeus, and labrum; pronotum with short hairs on anterior margin and numerous hairs of varying length on middle, sides, and rear; wing membranes and veins with numerous short hairs but without punctations or micrasters; tergites with numerous bristles and hairs, some long and some about half of the length of the longest bristles; sternites with numerous long hairs and bristles. Head oval, somewhat elongate; line between ocelli widely and evenly concave in middle and convex near ocelli; middle of head depressed near fontanelle; fontanelle spot somewhat triangular or elliptical, smaller than ocellus, length about equal to width. Eye large, nearly circular, about one-twentieth to one-seventh of its diameter from lower margin of head. Ocellus large, oval, about its width or less than its width from eye. (The measurements of the ocellus and its distance from the eye in Emerson,

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF MANY SOLDIERS OF *Labiotermes labralis* (HOLMGREN)

	Lecto-type, Peru	Para-lecto-type, Peru	Central Amazonas, Brazil	Colombia, Bolivia, Brazil, British Guiana, Trinidad
Length of head to tip of mandibles	3.76	—	4.15–4.90	3.81–4.68
Length of head to tip of labrum	3.18	4.27	4.01–4.56	3.47–3.97
Length of head to side base of mandible	2.29	3.05	3.29–3.51	2.85–3.14
Width of head	1.90	2.50	2.63–2.82	2.24–2.48
Thickness of head, including tube and post-mentum	1.53	2.00	1.94–2.29	1.86–2.09
Length of frontal tube (approximate)	0.12	0.15	0.16–0.21	0.16–0.24
Diameter of tip of frontal tube	0.15	0.18	0.21–0.26	0.23
Length of postmentum	1.29	1.68	1.72–1.82	1.12–1.75
Maximum width of postmentum	0.68	0.85	0.78–0.99	0.68–0.73
Minimum width of postmentum	0.53	0.68	0.57–0.80	0.47–0.55
Length of labrum in middle	0.86	1.02	0.80–1.11	0.61–0.87
Width of labrum	0.69	0.88	0.80–0.92	0.73–0.85
Length of left mandible	1.47	1.87	1.72–1.84	1.51–1.71
Length of pronotum	0.59	—	0.71–0.80	0.76–0.87
Width of pronotum	1.05	—	1.30–1.58	1.22–1.51
Length of hind tibia	1.71	—	2.24–2.43	1.94–2.25

1925, p. 364, are erroneus.) Antenna with 17 articles, third slightly longer than fifth and about two-thirds as long as second, fourth shorter than fifth. Postclypeus strongly convex in profile, slightly depressed in middle, median line distinct, length about equal to or a little longer than half of its width. Pronotum relatively wide, about four-fifths to nine-tenths of width of head, front margin slightly concave from above and often peaked or pointed in middle from rear, posterior margin strongly emarginate, sides and angles rounded. Mesonotum and metanotum with deeply emarginate hind margins, each forming angle of about 115 degrees.

COMPARISONS: *Labiotermes brevilabius* is smaller throughout, has an elongated, slit-shaped, fontanelle spot, and has 16 articles in the antenna. *Labiotermes longilabius* in general is somewhat smaller, has an oval fontanelle forked at the tip, and the head elevated in the region of the fontanelle.

SOLDIER (FIGS. 3, 4): Head light brownish yellow, slightly darker on sides of frontal tube, much darker at side margins of front; postmentum about same color as head, side margins light brown; tip of frontal tube

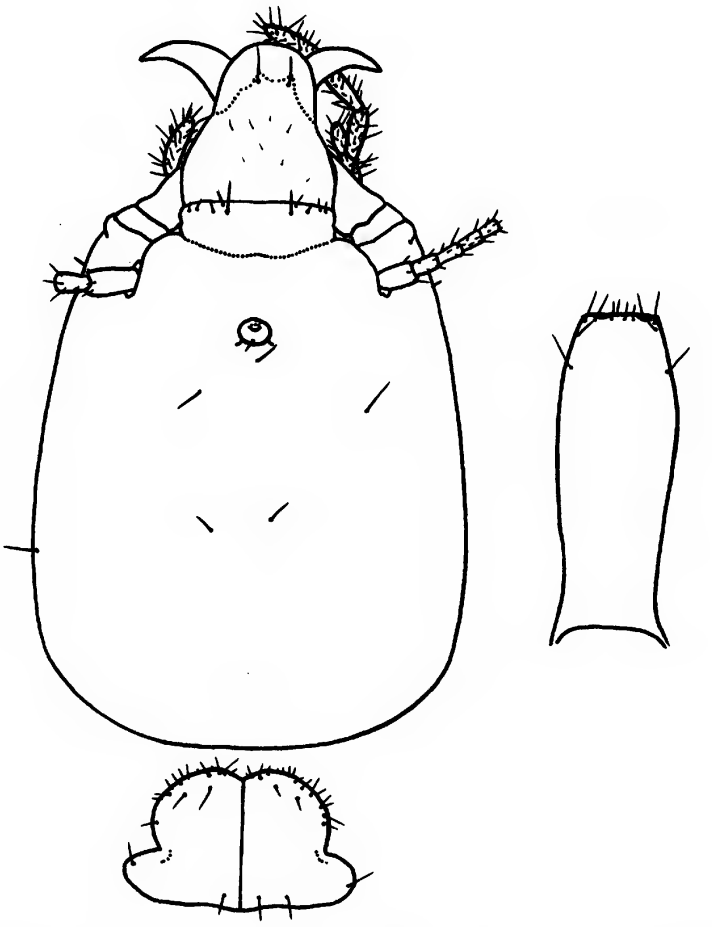

FIG. 3. Soldier of *Labiotermes labralis* (Holmgren), upper New River, British Guiana; head and pronotum from above and postmentum from below.

white; antenna light yellowish brown to yellow, lighter than head; postclypeus color of head; hind portion of labrum brown; front portion of labrum light yellow or light brown, with a broad white tip; pronotum light tan to yellow; coxae and femora yellowish tan; tibiae yellowish white; tergites and sternites yellow to white. Head, clypeus, and labrum with a few sparsely arranged bristles; tip of frontal tube without hairs; postmentum with a few bristles in front and along sides near front; labrum usually but not in all cases with two stout bristles at front of sclerotized portion behind white tip, and a few small hairs in middle; pronotum with

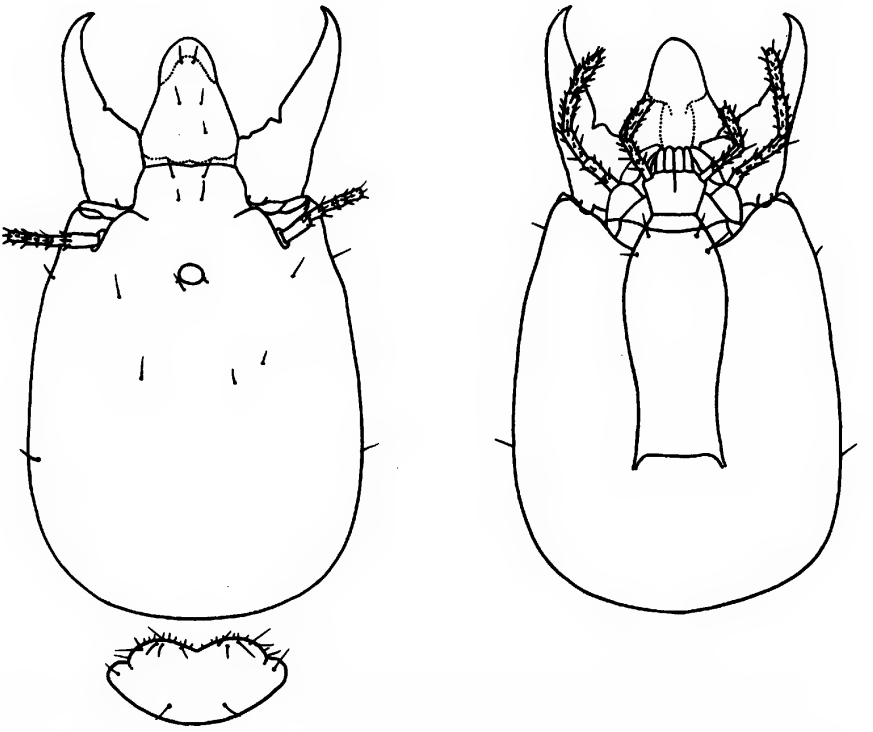

FIG. 4. Soldier of *Labiotermes labralis* (Holmgren), near Manaos, Brazil; head from above and from below, and upper surface of pronotum tilted backward.

a few short hairs on front margin and a few fairly long bristles on or near all margins; tergites with bristles and hairs, posterior tergites with numerous scattered long bristles and hairs about half of length of bristles; sternites with pilosity similar to that of posterior tergites. Head subrectangular, narrowed in front, sides and hind margin convex, side margins near antennae bases slightly concave or not, hind angles widely rounded, more or less rounded bump above each antenna base; small frontal tube in middle behind level of antennae bases, length of tube about equal to or one and one-fourth times as long as diameter of tip; postmentum long, length about two and one-fifth to two and one-half times its maximum width, maximum width about one and one-fourth to one and three-fourths times minimum width at constriction, profile strongly convex. Antenna with 15 or 16 articles, third in some cases in process of dividing. Labrum slightly longer than broad, tip rounded, sides strongly concave at junction of basal and apical portions, sides strongly convex near base. Mandibles

curved near tips, with some variation in degree of curvature, outer margin of left mandible straight immediately behind curved tip, outer margin of right mandible slightly concave in middle, dentition as shown in figure 4. Pronotum with large front lobe, front margin conspicuously emarginate, with a wide median notch, posterior margin somewhat irregular, lobe of pronotum in profile forming an angle of about 135 to 160 degrees with the middle portion. Outer edge of front coxa slightly convex in outline, with a stronger convexity at the base but without a conspicuous projection or hump present, in contrast with other species.

COMPARISONS: All other species have the frontal tube in a more forward position at or close to the line between the bases of the antennae, the tip of the frontal tube with many hairs, and a projection or hump at the side base of the front coxa. *Labiotermes brevilabius* is in general smaller and has a relatively shorter labrum and relatively more bristles on the head. *Labiotermes longilabius* is a little smaller in most measurements and has straighter sides of the head. *Labiotermes pelliceus* has a much more hairy head and the sides of the labrum more evenly curved.

VARIATION WITHIN THE SPECIES: The imagoes vary to some extent in the size, the relative size of the ocelli and eyes, the distance of the ocellus from the eye, the degree of the elevation and depression of the head between the ocelli, and the presence or absence of a small point in the middle of the front margin of the pronotum.

The soldiers vary considerably in the size of the head, the presence or absence of a slight constriction of the head near the bases of the antennae, the presence or absence of two conspicuous bristles at the front margin of the sclerotized portion of the labrum, the degree of curvature of the tips of the mandibles, the number of antennal articles, and the shape of the postmentum.

In the earlier stages of this study, an attempt was made to distinguish subspecies or species on the basis of these variations, particularly as the species of termitophiles of the genus *Termitozyras* from Trinidad, British Guiana, and Bolivia show distinctions. However, the variation of the termites did not show geographic consistency in most instances, and the slight consistency that was detected was based on too few specimens and was of such a nature that geographic races were not clearly distinguishable. In general, the number of specimens of both the reproductive castes and the soldiers from a wide range of localities should have been sufficient to indicate geographic races, subspecies, or species populations if they occurred (Emerson, 1935). The decision was made, therefore, to place *Labiotermes labralis labralis* and *L. labralis boreus* Emerson in synonymy with *L. labralis* (Holmgren), at least until more evidence indicates ade-

quate taxonomic distinctions. The large soldiers from Manaos, Amazonas, Brazil, and vicinity likewise do not deserve nomenclatural distinction with our present information.

LOCALITIES AND SPECIMENS: Type locality, Chaquimayo (latitude 13° 25′ S., longitude 70° 27′ W.), Peru, one female dealate (morphotype selected by A. E. Emerson), one soldier (lectotype selected by A. E. Emerson), "*Cornitermes labralis*" determined and collected by N. Holmgren, deposited in the Naturhistoriska Riksmuseum, Stockholm, Sweden; one male dealate (paramorphotype selected by A. E. Emerson), one soldier (paralectotype selected by A. E. Emerson), "*Cornitermes labralis*" determined and collected by N. Holmgren. Cachuela Esperanza (latitude 11° 32′ S., longitude 66° 54′ W.), Bolivia, soldiers, workers, "*Cornitermes* (*Labiotermes*) *labralis*" determined by T. E. Snyder, collected by W. M. Mann. Finca of Captain Series (latitude 2° 45′ N., longitude 71° 00′ W.), Rio Guaviare, Colombia, one soldier, workers, collected by S. Weinstein, December, 1957. Villavicencio (latitude 4° 17′ N., longitude 73° 43′ W.), Meta, Colombia, king, queen, soldiers, workers, collected by C. H. Seevers, Nos. 12, 23, July 14, 23, 1938. Moitaco (latitude 8° 00′ N., longitude 64° 45′ W.), eastern Bolivar, Venezuela, one soldier, workers, collected by P. J. Anduze, September 18, 1940. (This locality is in a savanna region on general vegetation maps; probably the precise site of the collection is in a gallery forest.) São Gabriel (latitude 0° 12′ S., longitude 67° 01′ W.), Rio Negro, Brazil, one soldier, one worker, collected by A. Roman, January 3, 1924. Manaos (latitude 3° 06′ S., longitude 60° 00′ W.), Amazonas, Brazil, one soldier, one worker, collected by A. Roman, May 14, 1915. Lago Poraquequáre, Manaos (latitude 3° 06′ S., longitude 60° 00′ W.), Amazonas, Brazil, one soldier, one worker, collected by A. Roman, May 14, 1915. Taracuá (latitude 0° 06′ N., longitude 68° 23′ W.), Rio Waupes or Rio Uapés, Amazonas, Brazil, soldiers, workers, collected by A. Roman, March 24, 1924. Rio Autaz (latitude 3° 20′ to 5° 00′ S., longitude 58° 45′ to 60° 00′ W.), Amazonas, Brazil, two soldiers, one worker, collected by A. Ries, August 24, 1914. Itabu Creek (latitude 1° 42′ N., longitude 57° 55′ W.), tributary of upper New River, Acary Mountains, British Guiana, two imagoes, one soldier, workers, collected by E. R. Blake, October, 1938. Above Wanatabo (Wototototobo) Falls (about latitude 4° 10′ N., longitude 57° 35′ W.), Courantyne River, British Guiana, queen, soldiers, workers, collected by N. Weber, No. 565.1, July 15, 1936. Rockstone (latitude 6° 03′ N., longitude 58° 40′ W.), British Guiana, imagoes, one soldier, workers, collected by G. E. Bodkin, April 11, 1914. Kartabo (latitude 6° 50′ N., longitude 58° 42′ W.), British Guiana, imagoes, queens, soldiers, workers, collected

by A. E. Emerson, No. 142, July 24, 1920, No. 24.85, March 29, 1924, No. 24.142, May 12, 1924. St. Joseph (latitude 10° 40′ N., longitude 61° 23′ W.), Trinidad, the West Indies, king, queen, soldiers, workers, collected by A. E. Emerson, No. 503, November 27, 1920. North Range (about latitude 10° 45′ N., longitude 61° 20′ W.), Trinidad, the West Indies, imagoes, one soldier, workers, collected by A. M. Adamson, No. 1198, June 4, 1936. Mt. Tabor (not located), Trinidad, the West Indies, queen, soldiers, workers, collected by E. McCallan, J. T. Davey, and G. Williams, in forest at 1800 feet in elevation, December 15, 1945. Arena Forest (not located), Trinidad, recorded by Seevers (1957).

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF A COTYPE FEMALE IMAGO OF *Labiotermes longilabius* (SILVESTRI)

Length of head to tip of labrum	1.94
Length of head to side base of mandible	1.33
Width of head	1.75
Length of fontanelle	0.16
Width of fontanelle	0.12
Fontanelle from ocellus	0.38
Diameter of eye	0.59
Eye from lower margin of head	0.04
Ocellus from eye	0.02
Length of ocellus	0.29
Width of ocellus	0.21
Length of postclypeus	0.41
Width of postclypeus	0.82
Length of pronotum	1.04
Width of pronotum	1.63
Length of hind tibia	2.09
Length of forewing scale	1.00
Length of forewing from suture	14.48
Width of forewing	4.80

Labiotermes longilabius (Silvestri)

Cornitermes longilabius SILVESTRI, 1901, p. 5 (imago).

Cornitermes longilabius SILVESTRI, 1903, pp. 59 (imago, soldier, worker), 127 (biology), text fig. 13 (wings), pl. 3, figs. 103, 104, 105 (imago, soldier, worker).

Termes (*Termes*) *longilabius* DESNEUX, 1904, p. 37 (synonymy).

Cornitermes (*Labiotermes*) *longilabius* HOLMGREN, 1912, pp. 49, 50 (systematics), text fig. 21 (imago mandible).

Labiotermes longilabius SNYDER, 1949, p. 334 (synonymy).

IMAGO (FIG. 5): Head generally medium reddish brown; fontanelle light yellow; postclypeus slightly lighter than head; labrum lighter than postclypeus, tip hyaline; antennae light brown; front of pronotum lighter than head, rear almost as dark as head; mesonotum and metanotum about same color as pronotum; legs yellow-brown; portions of wing scale and interior edge of radius brown, costa and outer portions of radius yellow-brown; wing membrane yellowish hyaline; tergites and sternites yellow-brown. Head and postclypeus with a few medium long bristles and short hairs; pronotum with short hairs on front margin and medium long bristles and short hairs on side margins and middle portion; wing membrane and veins with short hairs but without punctations or micrasters; tergites with abundant hairs and bristles. Head oval; line between ocelli fairly evenly convex, with a small elevation in region of fontanelle; fontanelle spot small, with a forked anterior edge and a small depression in the center. Eye of medium size, close to lower margin of head. Ocellus large, widely oval, upper edge somewhat elevated, lower edge depressed, close to eye. Postclypeus arched, length about half of its width. Antenna with 17 articles, third about equal to fourth, fifth longer than fourth, second longer than fifth. Pronotum length about five-eighths of its width, sides convex and converging toward rear, front margin flatly irregular or almost straight from above, median line distinct and somewhat depressed, hind margin widely emarginate. Hind margins of mesonotum

TABLE 4

MEASUREMENTS (IN MILLIMETERS) OF A COTYPE SOLDIER OF *Labiotermes longilabius* (SILVESTRI)

Length of head to tip of mandible (approximate)	3.66
Length of head to tip of labrum	3.39
Length of head to side base of mandible	2.49
Width of head	1.88
Thickness of head including tube and postmentum	1.65
Length of frontal tube (approximate)	0.15
Diameter of tip of frontal tube	0.23
Length of postmentum	1.23
Maximum width of postmentum	0.58
Minimum width of postmentum	0.41
Length of labrum from side base	0.76
Width of labrum	0.59
Length of left mandible	1.35
Length of pronotum	0.67
Width of pronotum	1.01
Length of hind tibia	1.49

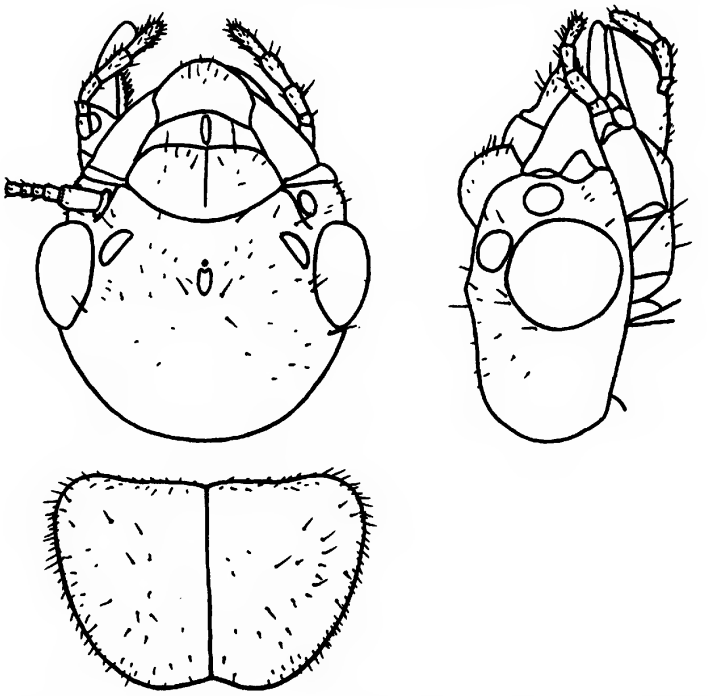

FIG. 5. Cotype female imago from type colony of *Labiotermes longilabius* (Silvestri), Coxipó, Brazil; head and pronotum from above and head from the side.

and metanotum widely emarginate, median angle 125–135 degrees, lateral angles greater than right angles.

COMPARISONS: *Labiotermes brevilabius* is the closest species but has a pattern of light areas on the head, the posterior region of the pronotum not so dark, fewer bristles and more short hairs on the head and pronotum, more short hairs on the front coxa, a somewhat more depressed area between the ocelli, smaller and less conspicuous fontanelle spot not so elevated above the general surface of the head, the eye smaller and farther from the ocellus, the antenna with 16 articles, a slightly less indented hind margin of the pronotum, and narrower wings.

SOLDIER (FIG. 6): Head and postmentum yellow-brown; labrum darker than top of head and equal to darker portions of front, tip whitish hyaline; antennae yellow-brown; outer portions of mandibles dark brown; pronotum light yellow-brown; legs uniform light yellow-brown. Head with a few bristles on front half, at opening of frontal gland, and front part of labrum behind tip; postmentum with a few bristles near anterior margin and a few very short inconspicuous hairs on anterior third; pronotum

with short hairs and a few bristles around front margin and sides, with one bristle on each side of central rear portion; tergites covered with medium length bristles and hairs of medium length; sternites like tergites except bristles longer and more differentiated from hairs. Head elongate and somewhat rectangular, a little wider behind than in front, sides slightly concave at level of antennae bases and slightly convex in middle; frontal tube comparatively thick and projecting; profile of head fairly flat on top, with a slightly upturned frontal tube; profile of postmentum evenly convex. Antenna with 15 articles, third, fourth, and fifth of about equal length, second longer than third. Labrum elongate, with a hyaline

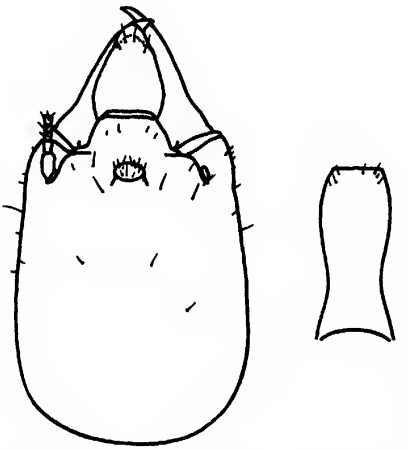

FIG. 6. Cotype soldier from type colony of *Labiotermes longilabius* (Silvestri), Coxipó, Brazil; head from above and postmentum from below.

or white tip and strongly convex sides near base. Each mandible with V-shaped indentation in front of first marginal tooth, indentation smaller in left mandible than in right. Pronotum with a large frontal lobe, front margin emarginate, profile with a shallow angle between frontal lobe and somewhat convex disc. Front coxa with a blunt projection on outer side near base.

COMPARISONS: The closest species is *L. brevilabius*, which differs in its smaller general size, its proportionately less thick head, its larger number of bristles on the head, its slightly shorter frontal tube, its less convex postmentum in profile, its shorter labrum, the proportionately shorter frontal lobe of the pronotum, and the sharper projection of the front coxa near its base.

LOCALITIES AND SPECIMENS: Type locality, Coxipó (latitude 15° 30′ S., longitude 56° 00′ W.), Cuiabá, Mato Grosso, Brazil, one female imago cotype, one soldier cotype, workers, from type colony, "*Cornitermes longi-*

labius," determined and collected by F. Silvestri, August-September, 1900. Corumbà (latitude 19° 00′ S., longitude 57° 25′ W.), Mato Grosso, Brazil, Silvestri (1903, p. 59).

Labiotermes brevilabius, new species

Labiotermes sp. ARAUJO, 1958a, p. 200 (locality).

IMAGO (FIG. 7): Head generally medium reddish brown, with light

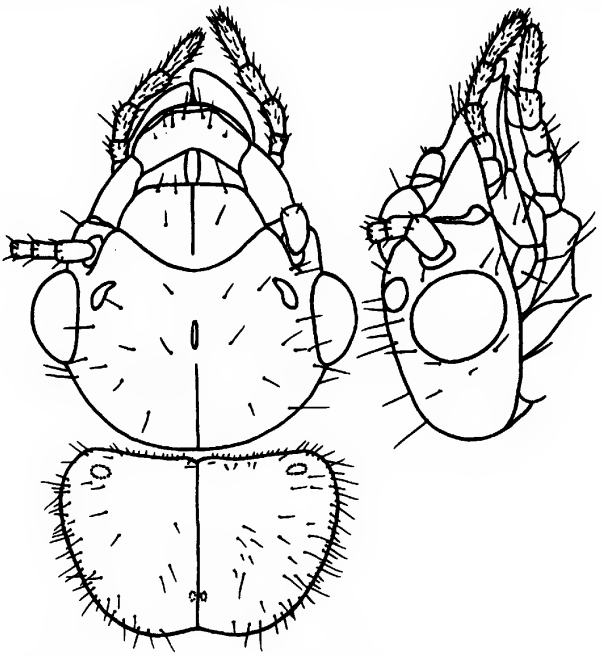

FIG. 7. Paramorphotype male imago from type colony of *Labiotermes brevilabius*, new species, Novo Horizonte, São Paulo, Brazil; head and pronotum from above and head from the side.

areas in middle and behind eyes; antennae light brownish yellow, slightly lighter than postclypeus; postclypeus light brown, lighter than head; labrum same color as postclypeus, with a broad hyaline tip; pronotum light brown; mesonotum and metanotum about same color as pronotum; portions of wing scales dark brown; wing membrane yellowish hyaline, subcosta and radius as dark as wing scale along most of wing length; under side of thorax, coxae, and femora light yellowish tan; tibiae light brown, slightly darker than femora; tergites light brown; sternites light

TABLE 5
MEASUREMENTS (IN MILLIMETERS) OF TWO IMAGOES OF
Labiotermes brevilabius, NEW SPECIES

	Morphotype Female	Paramorphotype Male
Length of head to tip of labrum	1.76	1.68
Length of head to side base of mandible	1.27	1.06
Width of head	1.59	1.56
Length of fontanelle	0.12	0.15
Width of fontanelle	0.02	0.03
Fontanelle from ocellus	0.49	0.43
Diameter of eye	0.47	0.49
Eye from lower margin	0.05	0.08
Ocellus from eye	0.10	0.09
Length of ocellus	0.22	0.21
Width of ocellus	0.17	0.15
Length of postclypeus	0.44	—
Width of postclypeus	0.65	—
Length of pronotum	0.85	0.80
Width of pronotum	1.38	1.37
Length of hind tibia	1.94	1.88
Length of forewing scale	0.85	0.80
Length of forewing from suture	13.41	13.35
Width of forewing	3.66	3.72

brownish yellow toward front, shading to light brown almost as dark as tergites toward rear. Head and postclypeus with a few long bristles; labrum with several bristles on front and sides; pronotum with few scattered hairs and bristles in middle, front margin with numerous short hairs, side margins with numerous hairs and bristles; wing membrane and veins with short hairs but without punctations or micrasters; tergites with a few bristles and many hairs almost as long as bristles or shorter; sternites with numerous hairs and less numerous bristles about as long as those on tergites; membranous portion of abdomen on sides covered with many curved hairs. Head oval, somewhat elongate; line between ocelli convex on both sides near top of protruding ocelli and rather sharply concave and depressed in middle; fontanelle spot inconspicuous, slit-shaped, and depressed, four to five times as long as wide. Eye rather large, oval, one-sixth to one-tenth of its diameter removed from lower margin. Ocellus large, subelliptical, nearly as large as antennal socket, removed from eye by slightly more than one-half of its width. Antenna with 16 articles, third a little shorter than second, fourth equal to or slightly shorter than third. Postclypeus longer than half of its width. Pronotum almost nine-

TABLE 6
MEASUREMENTS (IN MILLIMETERS) OF THIRTY SOLDIERS OF *Labiotermes brevilabius*, NEW SPECIES

	Holotype	Paratypes	Mean
Length of head to tip of mandible	3.32	2.81–3.40	3.08
Length of head to tip of labrum	2.79	2.59–3.03	2.80
Length of head to side base of mandible	2.20	1.98–2.50	2.24
Width of head	1.66	1.46–1.75	1.60
Thickness of head including tube and postmentum	1.41	1.25–1.42	1.36
Length of frontal tube	0.12	0.12–0.24	0.17
Length of postmentum	1.23	1.18–1.35	1.25
Maximum width of postmentum	0.53	0.46–0.54	0.52
Minimum width of postmentum	0.35	0.28–0.35	0.32
Length of labrum from side base	0.47	0.43–0.68	0.51
Width of labrum	0.57	0.52–0.57	0.54
Length of left mandible	1.18	1.04–1.18	1.12
Length of pronotum	0.59	0.52–0.66	0.59
Width of pronotum	1.02	0.80–1.06	0.98
Length of hind tibia	1.47	1.30–1.56	1.43

tenths as wide as head, with converging, somewhat curved sides and slightly emarginate front and hind margins, median line distinct. Mesonotum and metanotum with deeply emarginate hind margins, with a median angle of about 125 degrees.

COMPARISONS: *Labiotermes longilabius* is the closest species (see comparisons of the imago of *L. longilabius*). *Labiotermes labralis* is larger, has a subtriangular fontanelle spot, and has 17 articles in the antenna.

SOLDIER (FIG. 8): Head yellow to light red-brown; postmentum about color of top of head, darker along lateral margins; antenna yellow; postclypeus about color of top of head; labrum same color as top of head, darker along sides, with broad whitish tip; outer portion of mandible dark brown, almost black, basal portion dark brownish orange, darker than head; hind part of pronotum and posterior portion of frontal lobe light yellowish tan, front part of frontal lobe yellow; legs, tergites, and sternites yellow. Head and labrum with numerous bristles, opening of frontal tube with ring of short hairs; postmentum with few bristles and a number of minute hairs on front half; postclypeus with a few bristles; front margin of pronotum with numerous bristles and hairs, hind margin with few bristles near lateral angles, central areas of both frontal lobe and base almost devoid of hairs and bristles; tergites and sternites with numerous hairs, those of sternites slightly longer than those of tergites. Head subrectangular, narrowed slightly in front, sides and posterior

margin somewhat convex, posterior angles broadly rounded; frontal tube comparatively short, midway between bases of antennae. Postmentum length about two and two-fifths times its maximum width, maximum width about one and three-fifths times minimum width. Antenna with 15 articles, fifth shorter than second but longer than third, fourth shortest or about equal to third; in most specimens third and fourth articles indistinctly divided to form a unit slightly longer than second but shorter than first article. Labrum relatively short, with moderately convex sides, in some cases retracted so as to appear shorter. Pronotum with large anterior lobe, front margin conspicuously emarginate, hind margin straight or slightly concave but not emarginate, profile with base and

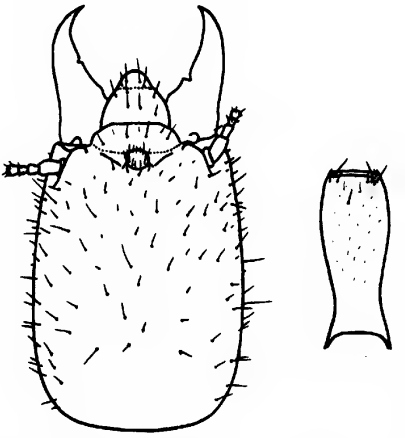

FIG. 8. Holotype soldier of *Labiotermes brevilabius*, new species, Novo Horizonte, São Paulo, Brazil; head from above and postmentum from below.

frontal lobe almost in line, forming an angle of about 170 degrees. Front coxa with a conspicuous but small projection on outer edge near base.

COMPARISONS: *Labiotermes longilabius* is the closest species. It is slightly larger, has a slightly longer frontal tube, the narrowest part of the postmentum proportionately wider, the labrum proportionately longer, and the projection at the base of the coxa more blunt at the tip. Both *L. longilabius* and *L. brevilabius* have a relatively shorter front of the head, with a more forward position of the frontal tube as compared with that of *L. labralis*. *Labiotermes pelliceus* has a much more hairy head.

LOCALITIES AND SPECIMENS: Type locality, Novo Horizonte (latitude 21° 28′ S., longitude 49° 13′ W.), São Paulo, Brazil, two imagoes (morphotype and paramorphotype), soldiers (holotype and paratypes), workers, nymph, collected by R. L. Araujo, No. 2652, November 24, 1944, "sandy nest of uniform structure." São Paulo (latitude 23° 33′ S., longitude 46° 38′ W.), São Paulo, Brazil, three soldiers (paratypes), workers, collected

TABLE 7
MEASUREMENTS (IN MILLIMETERS) OF SIX SOLDIERS OF *Labiotermes pelliceus*, NEW SPECIES

	Holotype	Paratypes
Length of head to tip of mandible	4.33	4.27-4.39
Length of head to tip of labrum	3.78	3.47-3.85
Length of head to side base of mandible	3.05	2.85-3.14
Width of head	2.53	2.37-2.53
Thickness of head	2.06	1.86-2.06
Length of frontal tube	0.18	0.15-0.18
Diameter of tip of frontal tube	0.37	0.35-0.38
Length of postmentum	1.59	1.27-1.59
Maximum width of postmentum	0.74	0.68-0.74
Minimum width of postmentum	0.55	0.47-0.55
Length of labrum in middle	—	0.71
Length of labrum from side base	—	0.83
Width of labrum	0.76	0.73-0.76
Length of left mandible	1.53	1.51-1.63
Length of pronotum	0.77	0.76-0.87
Width of pronotum	1.44	1.39-1.51
Length of hind tibia	1.97	1.94-2.08

by R. L. Araujo, No. 2907, September 25, 1945. Belo Horizonte (latitude 19° 51′ S., longitude 43° 57′ W.), Minas Gerais, Brazil, soldiers (paratypes), workers, nymphs, collected by R. L. Araujo, Nos. 3027, 3034, July 25, 1947. Lagôa Santa (latitude 19° 37′ 28″ S., longitude 43° 33′ 37″ W.), Minas Gerais, Brazil, soldiers (paratypes), workers, nymphs, collected by R. L. Araujo, No. 3400, January 24, 1952. São Sebastião do Paraizo (latitude 20° 55′ S., longitude 47° 00′ W.), Minas Gerais, Brazil, two soldiers (paratypes), soldier nymphs, collected by R. L. Araujo, No. 2811, February 21, 1945. Vespasiano, railroad stop northeast of Belo Horizonte (latitude 19° 41′ S., longitude 43° 56′ W.), Minas Gerais, Brazil, three soldiers (paratypes), workers, collected by R. L. Araujo, No. 3435, January 1, 1952.

Labiotermes pelliceus, new species

SOLDIER (FIG. 9): Front half of head and postmentum dark brown, rear half and under side of head lighter reddish brown; tip of frontal tube yellowish white; postclypeus about as dark as front of head, lighter near front margin; labrum light reddish brown, with a whitish hyaline tip; antennae light yellowish brown; mandibles dark brown along entire

length; pronotum and legs light brown; tergites and sternites light yellowish hyaline. Head, clypeus, labrum, and front half of postmentum thickly covered with hairs, rear half of postmentum with a few short hairs; tip of frontal tube with numerous hairs; tip of labrum without hairs; basal portion of mandible with numerous hairs; pronotum with short hairs on front margin and numerous hairs and bristles in middle and along side

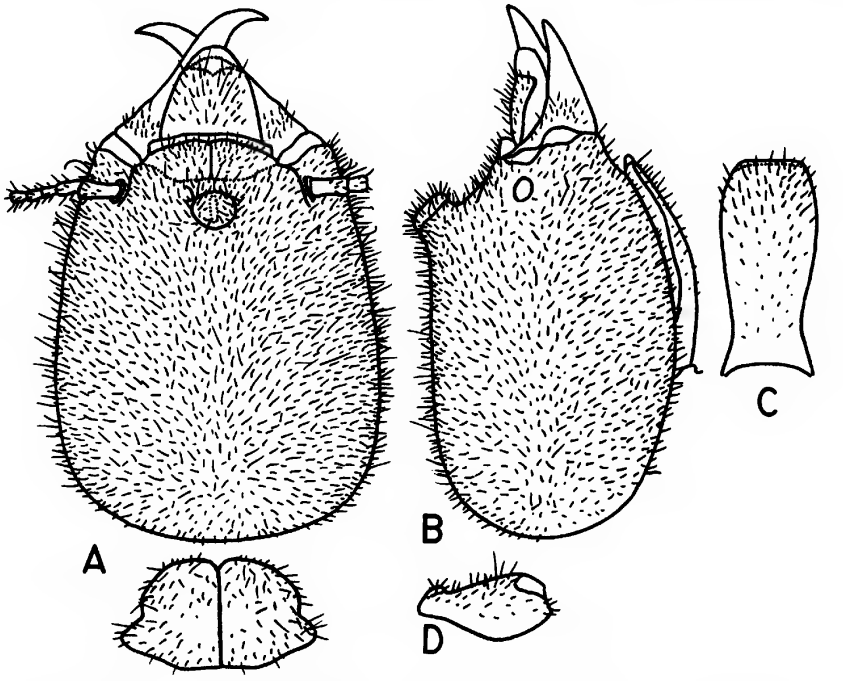

FIG. 9. Holotype soldier of *Labiotermes pelliceus*, new species, upper New River, British Guiana. A. Head and pronotum from above. B. Head from the side. C. Postmentum from below. D. Coxa of foreleg from the side.

margins; coxae and legs with numerous bristles and hairs; tergites and sternites with abundant hairs of varying length. Head subovoid, narrowed in front, sides and posterior margin convex, posterior angles broadly rounded; frontal tube short and wide, front margin of tube in line with bases of antennae. Postmentum elongated, constricted near posterior end, length more than twice maximum width, maximum width about one and one-third times minimum width. Antennae with 15 articles, third, fourth, and fifth about equal in length, each shorter than sixth. Labrum proportionately large. Tips of mandibles moderately curved,

right mandible with shallow notch about two-fifths of distance from condyle to tip, a single small tooth immediately behind notch; left mandible with a very small, V-shaped notch about two-thirds of distance from condyle to tip, a small triangular tooth about one-third of distance from condyle to tip. Pronotum with large, emarginate, frontal lobe, hind margin unevenly curved, in profile frontal lobe forming an angle of about 150–160 degrees with basal portion. Front coxa with a conspicuous but small rounded tubercle or projection on outer edge near base.

COMPARISONS: The dark-colored and hairy head of *L. pelliceus* is distinctive among the known species of the genus. *Labiotermes longilabius* and *L. brevilabius* are smaller. *Labiotermes pelliceus* is within the size range of *L. labralis*, but the position of the frontal tube and the coxal projection ally *L. pelliceus* to *L. longilabius* and *L. brevilabius*.

LOCALITIES AND SPECIMENS: Type locality, Itabu Creek (latitude 1° 42′ N., longitude 57° 55′ W.), tributary of upper New River, Acary Mountains, British Guiana, six soldiers (holotype and paratypes), workers, collected by E. R. Blake, October, 1938.

SUMMARY

The structure, relationships, phylogeny, distribution, origin, nests, ecology, and associated termitophiles of the South American termite genus *Labiotermes* are described and discussed. *Labiotermes labralis* (Holmgren) and *L. longilabius* (Silvestri) are redescribed and figured. *Labiotermes brevilabius*, new species, from Brazil, and *L. pelliceus*, new species, from British Guiana, are described and figured. A map showing the localities for each species and a key to the known species of imagoes and soldiers are included.

BIBLIOGRAPHY

ADAMSON, A. M.
1937. Preliminary report on termites and termite damage in Trinidad, West Indies. Trop. Agr., vol. 14, pp. 141–149.

AHMAD, M.
1950. The phylogeny of termite genera based on imago-worker mandibles. Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 37–86.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT
1949. Principles of animal ecology. Philadelphia and London, W. B. Saunders Co., xii+837 pp.

ARAUJO, R. L.
1954. Notes on the genus *Paracornitermes* Emerson, 1949, with the description of two new species (Isoptera, Termitidae, Nasutitermitinae). Rev. Brasileira Ent., vol. 1, pp. 181–189.

1958a. Contribuição à biogeografia dos térmitas de São Paulo, Brasil. Insecta-Isoptera. Arq. Inst. Biol., São Paulo, vol. 25, pp. 185–217.
1958b. Contribuição à biogeografia dos térmitas de Minas Gerais, Brasil. Insecta-Isoptera. *Ibid.*, vol. 25, pp. 221–236.

BATES, M.
1948. Climate and vegetation in the Villavicencio region of eastern Colombia. Geogr. Rev., vol. 38, pp. 555–574.

BEEBE, W.
1925. Studies of a tropical jungle. Zoologica, vol. 6, pp. 5–193.

BORGMEIER, T.
1950. Neue Gattungen und Arten termitophiler Staphyliniden aus Brasilien, nebst einem Katalog aller bisher aus der neotropischen Region beschreibenen Arten (Col. Staph.). Rev. Ent., vol. 21, pp. 625–676.

DAVIS, T. A. W., AND P. W. RICHARDS
1933–1934. The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest. Parts I and II. Jour. Ecol., vol. 21, pp. 350–384; vol. 22, pp. 106–155.

DESNEUX, J.
1904. Isoptera. Fam. Termitidae. *In* Wytsman, P. A. G., Genera insectorum. Brussels, fasc. 25, 52 pp.

EMERSON, A. E.
1925. The termites of Kartabo, Bartica District, British Guiana. Zoologica, vol. 6, pp. 291–459.
1928. Termites of the Belgian Congo and the Cameroon. Bull. Amer. Mus. Nat. Hist., vol. 57, pp. 401–574.
1935. Termitophile distribution and quantitative characters as indicators of physiological speciation in British Guiana termites. Ann. Ent. Soc. Amer., vol. 28, pp. 369–395.
1945. The neotropical genus *Syntermes* (Isoptera: Termitidae). Bull. Amer. Mus. Nat. Hist., vol. 83, pp. 427–472.
1952a. The biogeography of termites. *Ibid.*, vol. 99, pp. 217–226.
1952b. The neotropical genera *Procornitermes* and *Cornitermes* (Isoptera, Termitidae). *Ibid.*, vol. 99, pp. 475–540.
1955. Geographical origins and dispersions of termite genera. Fieldiana: Zool., vol. 37, pp. 465–521.
1960a. New genera of termites related to *Subulitermes* from the Oriental, Malagasy, and Australian regions (Isoptera, Termitidae, Nasutitermitinae). Amer. Mus. Novitates, no. 1986, pp. 1–28.
1960b. New genera on the *Subulitermes* branch of the Nasutitermitinae from the Ethiopian region (Isoptera, Termitidae). *Ibid.*, no. 1987, pp. 1–21.
1961. Vestigial characters of termites and processes of regressive evolution. Evolution, vol. 15, pp. 115–131.
1962. Vestigial characters, regressive evolution and recapitulation among termites. New Delhi, UNESCO Symposium on Termites in the Humid Tropics, 1960, pp. 17–30.

EMERSON, A. E., AND F. A. BANKS
1957. Five new species and one redescription of the neotropical genus *Armitermes* Wasmann (Isoptera, Termitidae, Nasutitermitinae). Amer. Mus. Novitates, no. 1841, pp. 1–17.

FANSHAWE, D. B.
1952. The vegetation of British Guiana. A preliminary review. Paper Imp. Forest Inst., Oxford Univ., no. 29, pp. 1-96.

GRASSE, P.-P., AND C. NOIROT
1954. *Apicotermes arquieri* (isoptère): ses constructions, sa biologie. Considérations générales sur la sous-famille des Apicotermitinae nov. Ann. Sci. Nat., Paris, Zool., ser. 11, vol. 16, pp. 345-388.

HARE, LAURA
1937. Termite phylogeny as evidenced by soldier mandible development. Ann. Ent. Soc. Amer., vol. 37, pp. 459-486.

HOLMGREN, N.
1906. Studien über südamerikanische Termiten. Zool. Jahrb., Abt. Syst., vol. 23, pp. 521-676.
1909. Termitenstudien I. Anatomische Untersuchungen. K. Svenska Vetensk.-Akad. Handl., vol. 44, no. 3, pp. 1-215.
1912. Termitenstudien III. Systematik der Termiten. Die Familie Metatermitidae. *Ibid.*, vol. 48, no. 4, pp. 1-166.

KRISHNA, K.
1963. The African genus *Foraminitermes* Holmgren (Isoptera, Termitidae, Termitinae). Amer. Mus. Novitates, no. 2161, pp. 1-23.

ROONWAL, M. L., AND O. B. CHHOTANI
1959. New neotropical element (*Anoplotermes*) in Indian termite fauna. Nature, vol. 184, no. 4703, pp. 1967-1968.
1960a. *Anoplotermes shillongensis* sp. nov., a new termite from Assam, India. Science and Culture, vol. 25, p. 701.
1960b. Soldier caste found in the termite genus *Speculitermes*. *Ibid.*, vol. 26, pp. 143-144.
1962. A new neotropical element (*Anoplotermes*) in the Indian termite fauna, with fuller description of *A. shillongensis* from Assam. Rec. Indian Mus., vol. 58, pp. 159-168.

SANDS, W. A.
1957. A revision of the East African Nasutitermitinae (Isoptera). Bull. Brit. Mus. (Nat. Hist.), Ent., vol. 5, pp. 1-28.

SEEVERS, C. H.
1957. A monograph on the termitophilous Staphylinidae (Coleoptera). Fieldiana: Zool., vol. 40, pp. 1-334.

SILVESTRI, F.
1901. Nota preliminare sui Termitidi sud-americani. Boll. Mus. Zool. Anat. Comp. Torino, vol. 16, no. 389, 8 pp.
1903. Contribuzione alla conoscenza dei Termitidi e Termitofili dell'America meridionale. Redia, vol. 1, pp. 1-234.

SJOSTEDT, Y.
1926. Revision der Termiten Afrikas 3. Monographie. K. Svenska Vetensk.-Akad. Handl., vol. 3, no. 1, pp. 1-419.

SNYDER, T. E.
1926. Termites collected on the Mulford biological exploration to the Amazon basin, 1921-1922. Proc. U. S. Natl. Mus., vol. 68, art. 14, pp. 1-76.
1949. Catalog of the termites (Isoptera) of the world. Smithsonian Misc. Coll., vol. 112, pp. 1-490.

1956. Termites of the West Indies, the Bahamas, and Bermuda. Jour. Agr. Univ. Puerto Rico, vol. 40, pp. 189–202.

WARMING, E.

1925. Oecology of plants. London, Oxford University Press, xi+422 pp.